THE DENTITION AND MUSCULATURE OF SOME MIDDLE ORDOVICIAN (LLANDEILO) BIVALVES FROM FINISTÈRE, FRANCE

by MARGARET A. BRADSHAW

ABSTRACT. The dentition and musculature of palaeotaxodontid and palaeoheterodontid bivalves from the Middle Ordovician of Finistère is described. These characters suggest that a number of species currently grouped in the genus *Ctenodonta* show closer affinity to *Cardiolaria*, *Praeleda*, and *Tancrediopsis*. The two species of *Praeleda* examined are considered to have had a reversed (nuculoid) orientation. The palaeoheterodontids *Redonia deshayesi* and *Actinodonta naranjoana* exhibit reduction of hinge teeth during ontogeny, due to fusion and resorption. An early Palaeozoic bivalve phylogeny is suggested, based on the development of the dentition within this fauna.

THE Middle Ordovician bivalves of the Crozon Peninsula (Finistère) have been referred to in many publications. Earlier work was summarized by Kerforne (1901), who attributed the forms present to species described from beds of similar age in Portugal and Spain (Ribeiro, Sharpe, and Jones 1853, de Verneuil and Barrande 1855). Subsequent work has been summarized and expanded by Babin (1966) in a major work on the Palaeozoic Mollusca of Brittany.

The present work is more detailed and restricted to bivalves. Particular attention has been given to the dentition and its development during ontogeny, and to accessory muscle scar patterns.

This study is based on material from coastal sections near La Mort Anglaise (831487 and 838495) and south-east of Crozon (912441). These grid references refer to square UU of the U.T.M. international grid. The most perfectly preserved bivalves are found as disarticulated valves in numerous thin fossil bands in shales, and are present as internal and external moulds. Isolated steinkerns sometimes occur outside these fossil bands. The most prolific beds were found in the Schistes de Morgat (Llandeilo). A more detailed description of the nature of these fossil bands and their constituents can be found in Bishop, Bradshaw, Renouf, and Taylor (1969).

The bivalves frequently show tectonic distortion, and identification on general shape alone is therefore unsound. The dentition, combined with the positioning of the accessory muscle scars, was found to be more reliable.

The Llandeilian bivalves of the Crozon Peninsula were listed by Babin (1966) as: Order Palaeotaxodonta: *Ctenodonta bussacensis* (Sharpe) 1853, *Ctenodonta ciae* (Sharpe) 1853, *Ctenodonta costae* (Sharpe) 1853, *Ctenodonta ribeiroi* (Sharpe) 1853, *Ctenodonta britannica* Babin 1966, *Palaeoneilo hopensacki* (de Verneuil and Barrande) 1855, *Palaeoneilo beirensis* (Sharpe) 1853, *Palaeoneilo ctenodontoides* Babin 1966; Order Pantodontida: *Actinodonta naranjoana* (de Verneuil and Barrande) 1855, *Redonia deshayesi* Rouault 1851, emend. Gouzien 1934.

The placing of many of the palaeotaxodontids in the genus *Ctenodonta* is not supported by a comparison with the type species, *Ctenodonta nasuta* (Hall). The

[Palaeontology, Vol. 13 Part 4, 1970, pp. 623–45.]

palaeotaxodontids of the Crozon Peninsula exhibit several small, but significant, differences amongst themselves, and a revised list of the more abundant palaeotaxodontids is suggested:

Sub-class PALAEOTAXODONTA
Order NUCULOIDA

Cardiolaria beirensis (Sharpe) 1853.
Tancrediopsis ezquerrae (Sharpe) 1853.
Praeleda ciae (Sharpe) 1853.
Praeleda costae (Sharpe) 1853.

Each genus of the fauna is reviewed separately in the following pages. As *Ctenodonta ribeiroi* and *Ctenodonta britannica* are inadequately represented in the material collected, they are not discussed. The description of each species refers to the actual shell, but the accompanying figures are of internal moulds, as the dentition in many cases was too delicate to withstand the making of latex casts.

In all accompanying illustrations the muscle scars are indicated as follows: Anterior adductor muscle—AA; Posterior adductor muscle—PA; accessory muscles—a. Other symbols used are explained in the figure captions. With incomplete specimens the suggested outline has been dotted in.

All figured specimens have been deposited in the museum of the Department of Geology, University of Canterbury, New Zealand.

Orientation. The orientation of the palaeotaxodontids was deduced from the nature of the teeth along the hinge line and the positions of the accessory muscle scars. Two orientations are present, a normal orientation as shown by *Cardiolaria beirensis* and *Tancrediopsis ezquerrae*, and a reversed (nuculoid) orientation shown by *Praeleda costae* and *Praeleda ciae*. A fuller explanation is given at the beginning of the section on the reversed forms.

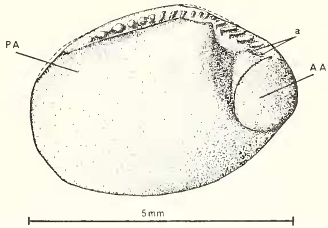
PALAEOTAXODONTIDS OF NORMAL ORIENTATION

Cardiolaria beirensis (Sharpe) 1853

Text-figs. 1–4

1853 *Nucula beirensis* Sharpe, p. 150, pl. 9, figs. 11–12.
1853 *Nucula bussacensis* Sharpe, p. 151, pl. 9, figs. 13–14.
1855 *Nucula hopensacki* de Verneuil and Barrande, p. 989, pl. 28, fig. 8.
1876 *Ctenodonta beirensis* de Tromelin and Lebesconte, p. 654.
1876 *Ctenodonta bussacensis* de Tromelin and Lebesconte, p. 683.
1886 *Ctenodonta beirensis* Barrois, p. 680.
1886 *Ctenodonta bussacensis* Barrois, p. 685.
1901 *Ctenodonta beirensis* Kerforne, p. 194.
1901 *Ctenodonta bussacensis* Kerforne, p. 195.
1901 *Ctenodonta hopensacki* Kerforne, p. 196.
1912 *Palaeoneilo hopensacki* Douville, p. 439, fig. 6.
1934 *Ctenodonta bussacensis* Gouzien, p. 179.
1966 *Ctenodonta bussacensis* Babin, p. 45, text-figs. 5 and 6; pl. 1, figs. 4 and 5.
1966 *Palaeoneilo hopensacki* Babin, p. 73, text-figs. 23 and 24; pl. 11, figs. 10 and 11.
1966 *Palaeoneilo beirensis* Babin, p. 74, text-figs. 25; pl. 11, fig. 9.

The general morphology and dentition of *Cardiolaria beirensis* is clearly illustrated in text-figs. 1–4. The most significant point concerning the dentition is the marked difference in adult forms between the anterior and posterior series of teeth. The anterior teeth are few (4–6 in adult), massive, and vary amongst themselves in shape, size and position. The posterior teeth are more numerous (15–20 in adult), uniform in size and placement, and usually chevron in shape. In the adult the posterior series of teeth tends to override the anterior, and there is resorption in this region. The dentition undergoes appreciable change during ontogeny. Recrystallization has destroyed the dentition of individuals smaller than 5 mm. in length and 3·5 mm. in height, but at this size the two series of teeth are almost indistinguishable, appearing continuous (text-fig. 1). With increase in size the two series of teeth become more distinct and discontinuous (text-fig. 2). With further growth the overriding of the first anterior tooth by the proximal end of the posterior series becomes emphasized, and the two series become separated by a narrow flat region (text-figs. 3 and 4).

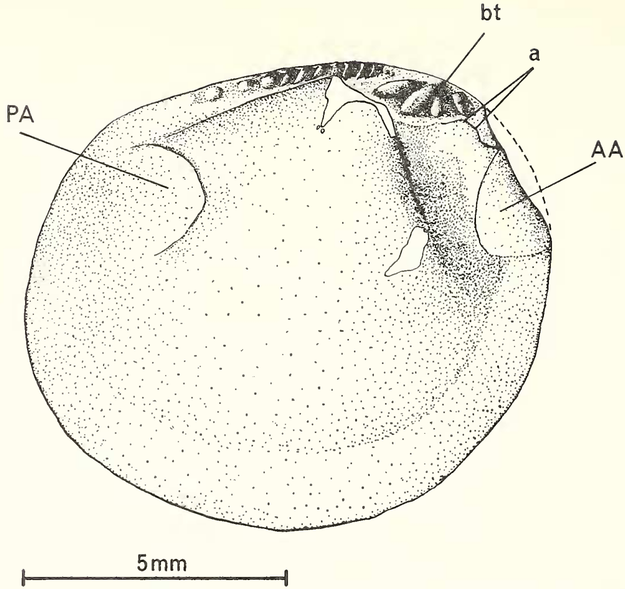


TEXT-FIG. 1. *Cardiolaria beirensis.* Internal mould of a juvenile right valve showing simple, continuous dentition. Pointed umbo missing. The unequally impressed musculature and the strong anterior myophoric plate are already distinct at this stage. Note the general similarity of tooth shape and size. The anterior teeth appear slightly thicker and more oblique to the dental plate. Specimen B. 10. Llandeilo. G.R. 838495.

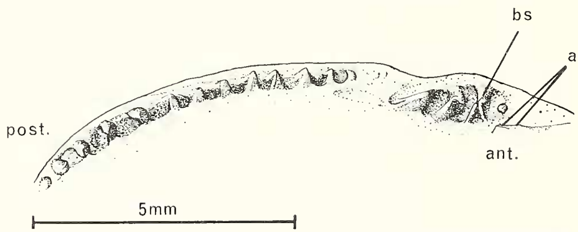
Fusion of anterior teeth in the left valve accompanies the growing discordance between the two series of teeth. In medium-sized individuals (approx. 1·3 cm. length, 1 cm. width) a bifid tooth opening ventrally is situated in the left valve. Certain specimens indicate that this bifid tooth is composed of a chevron tooth fused to a smaller, ridge-like tooth that lies ventral and posterior to it (illustrated by the opposite valve in text-fig. 3). In the right valve a corresponding spike-like tooth lies between two normally developed teeth, close to the ventral margin of the dental plate. In only one medium-sized valve has a bifid tooth been seen in the right valve. This specimen (text-fig. 2) was obtained from beds older than the bulk of the material studied. A larger valve of identical shape from the same horizon shows no trace of the bifid tooth.

In the largest forms available (text-fig. 4) the bifid tooth is retained, and the flat region between the two series of teeth appears prominent. This featureless area is interesting as *Cardiolaria* is the only palaeotaxodontid member of the Crozon Peninsula bivalve fauna to exhibit a well-marked area where resorption of teeth occurs. Bernard (1896) records the progressive resorption of teeth adjacent to the internal ligament of Tertiary and modern nuculids. The featureless area of *Cardiolaria beirensis* does not resemble the clearly defined resilifer of modern palaeotaxodontids, but it may indicate a very early stage in the migration of the external ligament onto the hinge plate.

The adductor muscle scars of *Cardiolaria beirensis* are rounded and equal in size, although the anterior scar is much more deeply impressed. The posterior pedal accessory muscle scar is too feeble to be visible, but those to the anterior, adjacent to the adductor scar, are very prominent. These accessory scars lie in the thickness of the myophoric plate where it abuts the hinge plate (text-figs. 1, 2). Most specimens appear to possess only one anterior pedal accessory muscle scar, but very well-preserved specimens

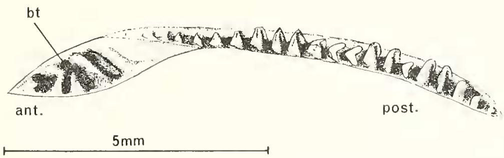


TEXT-FIG. 2. *Cardiolaria beirensis*. Young adult. Internal mould of right valve, umbonal region missing, showing the developing differences between the anterior and posterior series of teeth. The extreme posterior teeth are obscured. The mould of a bifid anterior tooth (bt—appearing as socket) and the position the two anterior pedal muscle scars are indicated. Specimen K.3. Llanvirn. G.R. 803469.



TEXT-FIG. 3. *Cardiolaria beirensis*. Internal mould of right valve (hinge only) showing anterior and posterior teeth and the area of resorption between them. The mould of an anterior bifid socket is indicated (bs). Specimen B.4. Llandeilo. G.R. 838495.

indicate it to be composed to two juxtaposed elliptical scars lying with their common long axes sub-parallel to the anterior part of the hinge plate. In these specimens a smaller scar is also present between the juxtaposed scars and the anterio-dorsal edge of the anterior adductor muscle scar. The close grouping of these scars is further indication of the normal orientation of *Cardiolaria*. The two elongate, juxtaposed scars



TEXT-FIG. 4. *Cardiolaria beirensis*. Internal mould of the hinge region only of a large left valve, showing the hinge plate clearly composed of two distinct dental sections. The few anterior teeth are massive, and the mould of a bifid tooth (bt) is indicated. The regular posterior teeth are numerous and vary from an asymmetrical chevron shape with a longer ventral limb, to ridge-like below the umbo. Both series of teeth show resorption where the posterior series overrides the anterior series. Specimen A.8. Llandeilo. G.R. 831487.

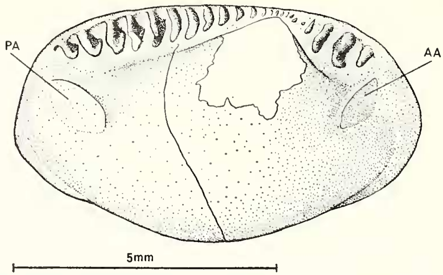
resemble the anterior protractor and retractor found in *Acila divaricata* figured by Driscoll (1964, fig. 3). The accompanying smaller scar in *Cardiolaria*, which is slightly ventral to these scars, is probably the smaller anterior protractor also visible in *Acila divaricata*.

Discussion. *Cardiolaria beirensis* is here interpreted as including *Ctenodonta beirensis*, *C. bussacensis*, and *C. hopensacki* of previous authors. Originally the three species were based on differences in general shape, but these characters alone have proved of little value in distorted faunas.

Babin (1966) has attempted to distinguish the species on the nature of the sub-umbonal teeth together with detailed variation in shape. However, he admits that without the sub-umbonal teeth the forms are difficult to distinguish in distorted faunas. Since the character of these teeth is related to stages in ontogeny, the maintenance of separate species can no longer be supported. Babin divides the three species into two genera, *Ctenodonta* and *Palaeoneilo*, which he places in two separate subfamilies, Ctenodontinae and Palaeoneilinae. He considers the former to be characterized by continuous teeth below the umbo and the latter by two series discontinuously arranged below the umbo.

However, McAlester (1968) describes the lectotype of *Palaeoneilo*, *Palaeoneilo constricta* (Conrad), as having 'fine taxodont dentition' a characteristic that is borne out by his illustrations (pl. 15, especially fig. 15). The teeth are continuous along the hinge, and the illustrated specimens appear in no way similar to *Ctenodonta hopensacki* or *C. beirensis*. Furthermore, the range of *Palaeoneilo* is generally accepted as being Devonian–Triassic.

The specific name *beirensis* is retained on the grounds of priority (Sharpe 1853, p. 150), but the species possesses no characters attributable to the type species of *Ctenodonta*, *Ctenodonta nasuta* (Hall). It does, however, show striking resemblances to the type species of *Cardiolaria* (*Cardiolaria barrandei*) figured by McAlester (1968, pl. 10), having the same distinct anterior myophoric plate and the two unequal series of teeth. For this reason *Ctenodonta beirensis* is here transferred to the genus *Cardiolaria*.



TEXT-FIG. 5. *Tancrediopsis ezquerrae*. Internal mould of a right valve, tilted to show the dental plate. The chevron-shaped posterior teeth decrease steadily in size towards the umbo below which they are ridge-like and low. The series is straight except just anterior of the umbo. The anterior teeth are fewer in number and show abrupt decrease in size at both ends of the series. The highest posterior tooth is equal in size to the highest anterior tooth. The junction of the two series is visible anterior of the umbo. Specimen A.12. Llandeilo. G.R. 831487.

Tancrediopsis ezquerrae (Sharpe) 1853

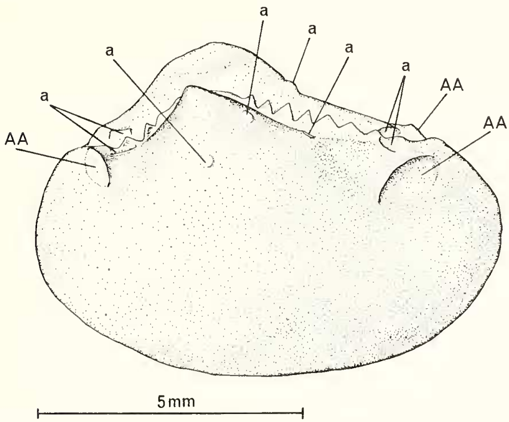
Text-figs. 5, 6

1853 *Nucula ezquerrae* Sharpe, p. 149; pl. 9, fig. 7.
1876 *Ctenodonta ezquerrae* de Tromelin and Lebesconte, p. 624.
1886 *Ctenodonta ezquerrae* Barrois, p. 680.
1901 *Ctenodonta ezquerrae* Kerforne, p. 196.
1966 *Ctenodonta costae* Babin, p. 52, text-figs. 13, 14, 15; pl. 1, figs. 6 and 7.

Unlike the other palaeotaxodontids of the fauna which possess teeth of different size and shape on each side of the umbo, the dentition of *Tancrediopsis ezquerrae* is very uniform in shape and size. The teeth are arranged in two series with more teeth present in the posterior series (text-fig. 5). The arrangement of the teeth on the two parts of the dental plate is closer to that in *Cardiolaria* than in *Praeleda*. The dentition appears continuous along the hinge plate but well-preserved specimens with the sub-umbonal region unobscured show that the two series are slightly offset (text-fig. 5). There is no indication of resorption in this region.

Young specimens of *Tancrediopsis ezquerrae* possess teeth that are pustule-like in shape rather than chevron. With increase in size of the individual the chevron shape develops with the formation of a strong groove down the side of the tooth facing away from the umbo.

The sub-equal adductor muscle scars are situated at the distal ends of the hinge plate beyond the last teeth. A distinct pedal accessory muscle scar is present close to each adductor muscle scar (text-fig. 6). In both cases the accessory scar lies adjacent to the edge of the hinge plate, and the posterior pedal scar is more obviously dorsal to its related adductor muscle scar than is the anterior pedal scar.



TEXT-FIG. 6. *Tancrediopsis ezquerrae*. Left side view of articulated internal moulds showing the characteristic oval shaped adductor muscle scars whose long axes converge ventrally, and the positions of the accessory muscle scars. Specimen 0·5. Llandeilo. G.R. 806468.

In addition three umbonal scars have been consistently observed. Two of these lie along the dorsal side of the umbonal cavity close to the hinge plate (text-fig. 6). The position of these scars is interesting as McAlester (1963) mentions faint impressions just below the posterior hinge plate in *Tancrediopsis contracta* which he suggests may represent pedal or visceral muscle scars. A further umbonal muscle scar lies ventrally placed in the umbonal cavity and is level with the adductor muscle scars.

Discussion. The general morphology of *Ctenodonta ezquerrae* of previous authors has little in common with the type species *Ctenodonta nasuta*, and it would seem more desirable to place the species in another genus.

McAlester (1963, p. 4) writes: 'The name *Tancrediopsis* will, however, probably prove useful in the future as a generic sub-division of the heterogeneous assemblage of Ordovician forms now included in "*Ctenodonta*".' It is suggested that *Ctenodonta ezquerrae* has closer affinities with *Tancrediopsis* than any other genus described to date.

The oval, dorsally impressed adductor muscle scars of *Ctenodonta ezquerrae* are very similar to those preserved in the type species *Tancrediopsis contracta* (Salter) which have long axes also converging ventrally. The strongly inflated valves, the regular but faint growth-lines, and the strong chevron teeth almost continuous along the hinge, are additional similarities. As in *Tancrediopsis contracta*, two distinct pedal muscle scars are present in *Ctenodonta ezquerrae* adjacent to the umbonal edge of the adductor muscle scars.

Although *Ctenodonta ezquerrae* does not possess the almost equilateral valves of the type species of *Tancrediopsis*, nor the two sub-equal series of teeth, the author feels that it has closer affinities to *Tancrediopsis* than to any other described genus of palaeotaxodontid, and transfers it accordingly.

PALAEOTAXODONTIDS OF REVERSE ORIENTATION

Orientation. A general discussion on the problem of palaeotaxodontid orientation would be inappropriate in a paper of this type. A separate contribution is in preparation.

However, with regard to the forms described here, the dentitions of *Praeleda* and *Cardiolaria* indicate that their orientations are opposite. In *Cardiolaria* the larger chevron teeth are always found along the shorter side of the valve on a plate whose inner edge is straight or arched dorsally (text-fig. 4). *Praeleda* is the reverse. The largest teeth are found on the longer side of the valve, but still on a plate whose inner edge is arched ventrally. The lower ridge-like teeth are present on a narrower plate, arched dorsally (text-fig. 7). It has been shown above that *Cardiolaria* has a normal orientation as indicated by the grouping of certain accessory muscle scars.

Where the shape of the teeth can be established in detail, the relative movement of the two valves can be determined and the position of the external ligament and regions of maximum opening inferred (the latter probably determined by the retraction of a large foot as in modern *Nucula*). The inferred positions in *Praeleda* and *Cardiolaria* are opposite.

Consequently, in the descriptions of *Praeleda*, the shorter end will be referred to as posterior, and the extended end as anterior.

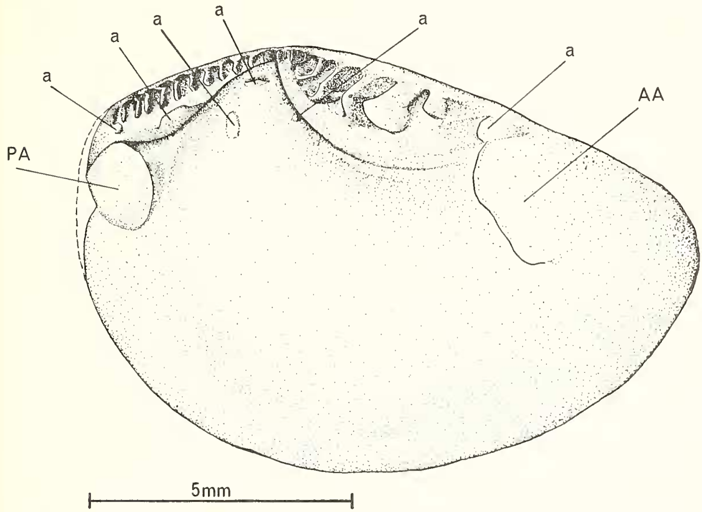
Despite tectonic distortion, *Praeleda costae* and *Praeleda ciae* can be readily distinguished from each other by the shape and disposition of the teeth and the relative positions of the accessory muscle scars.

Praeleda costae (Sharpe) 1853

Text-figs. 7–10

1853 *Nucula costae* Sharpe, p. 149, pl. 9, fig. 4.
1855 *Nucula costae* de Verneuil and Barrande, p. 989.
1876 *Ctenodonta costae*? de Tromelin and Lebesconte, p. 641.
1886 *Ctenodonta costae* Barrois, p. 680.
1891 *Ctenodonta costae* Barrois, p. 189, pl. 1, fig. 6.
1901 *Ctenodonta costae* Kerforne, p. 196.
1934 *Ctenodonta costae* Gouzien, p. 179.
1966 *Palaeoneilo ctenodontoides* Babin, p. 76, text-figs. 26–8; pl. 1, figs. 9–10; pl. 11, figs. 6, 12, 13.

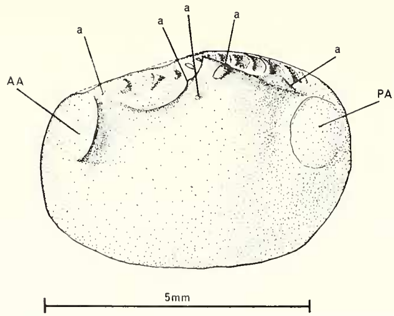
In *Praeleda costae* (text-fig. 7) the two series of teeth are arranged at an angle to each other on the hinge plate, the junction lying just anterior to the umbo. Seventeen to twenty-two teeth are usually present along the adult hinge, either divided equally between the two series or with more in the posterior series. Those in the anterior series are large and prominent, possessing an inconsistent chevron shape. The most anterior teeth commonly show the more usual curved chevron form with angles directed towards the umbo, but in many specimens the teeth closer to the umbo show a reversal of this shape with angles directed away from the umbo. The posterior teeth are low and ridge-like,



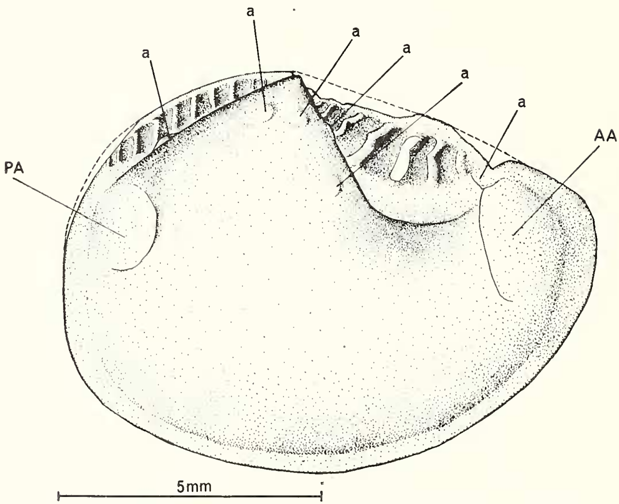
TEXT-FIG. 7. *Praeleda costae*. Internal mould of right valve, anterior to right, showing muscle scars and the two different types of teeth on each side of the umbo. Specimen 0·1. Llandeilo. G.R. 806468.

frequently curved with the concave side towards the umbo. In some cases the teeth appear to have a grossly asymmetrical form with the ventral limb developed at the expense of the dorsal limb. Where this form is visible the angle of the chevron is directed towards the umbo.

In juvenile forms of *Praeleda costae* (text-fig. 8) the adductor muscle scars are rounded and equal, but in the adult (text-fig. 7) the anterior adductor scar is larger and oval in shape with its long axis roughly parallel with the anterio-dorsal margin of the shell. In addition five pedal accessory muscle scars are usually visible. Three of these are umbonal in situation commonly arranged in the form of a triangle with its apex ventral and the base slanting downwards anteriorly. The scar closest to the umbo is frequently the strongest. A pedal accessory scar is present at the distal end of the anterior hinge plate, adjacent and dorsal to the anterior adductor muscle scar. Another prominent

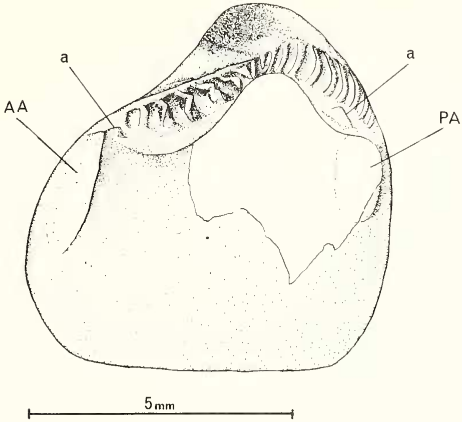


TEXT-FIG. 8. *Praeleda costae*. Internal mould of small left valve, anterior to left, showing early dentition and muscle scars. Specimen F.30. Llandeilo. G.R. 912441.



TEXT-FIG. 9. *Praeleda costae*. Internal mould of distorted right valve, anterior to right. Note accessory muscle scars. Specimen C.1.b. Llandeilo. G.R. 912441.

accessory scar lies half-way along, and ventral to, the posterior part of the hinge plate. This scar is quite isolated from the posterior adductor scar, and its position is characteristic of the species.



TEXT-FIG. 10. *Praeleda costae*. Internal mould of a distorted left valve, anterior to left, showing a more concordant junction between the two series of teeth than is usual for this species. Part of the external mould of a pronounced lunule is also visible. Specimen F.31.b. Llandeilo. G.R. 912441.

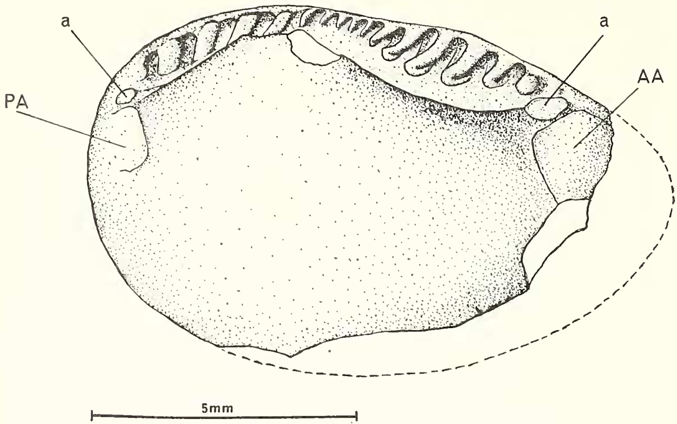
Praeleda ciae (Sharpe) 1853

Text-figs. 11, 12

1853 *Nucula ciae* Sharpe, p. 149, pl. 9, fig. 5.
1876 *Ctenodonta ciae* de Tromelin and Lebesconte, p. 641.
1886 *Redonia ciae* Barrois, p. 659.
1901 *Ctenodonta ciae* Kerforne, p. 195.
1923 *Ctenodonta ciae* Kerforne, p. 180.
1966 *Ctenodonta ciae* Babin, p. 49, text-figs. 10–12; pl. 1, fig. 9.

The teeth of *Praeleda ciae* are fewer than in *Praeleda costae*, and are arranged without disruption along the hinge plate (text-fig. 11). Approximately 16 teeth are present in the adult, either divided equally between the two series or with slightly more in the anterior series. The teeth of the anterior series have a clear, regular chevron form, curved in profile with angles directed towards the umbo. They merge steadily into the small ridge-like sub-umbonal teeth, which in turn pass posteriorly into the low, ridge-like posterior teeth.

In the adult the adductor muscle scars are unequal, the anterior scar being larger and oval in shape with its long axis roughly parallel with the anterio-dorsal margin of the shell. Five pedal accessory muscle scars are generally visible. Two of these are found dorsal and adjacent to both adductor muscle scars. A further three scars are present in the umbonal region, usually situated in a straight line slanting downwards towards the anterior. The lowest scar is frequently the strongest.

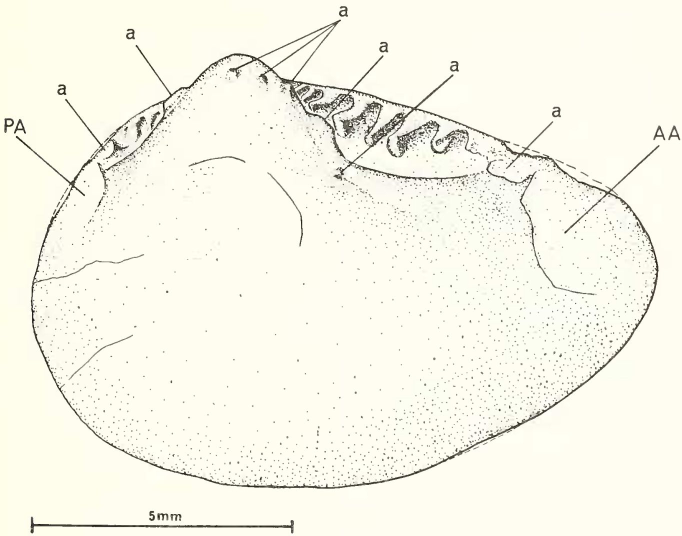


TEXT-FIG. 11. *Praeleda ciae*. Internal mould of right valve, anterior to right and tip of umbo missing. The anterior teeth are prominent and curved, the posterior teeth lower and ridge-like. The two series are continuous below the umbo where the teeth are low and ridge-like. Specimen B.19. Llandeilo. G.R. 838495.

Comparisons. *Praeleda costae* is particularly interesting as it is the more variable of the two species and sometimes exhibits a dental plate similar to that of *Praeleda ciae*, e.g. text-fig. 10. The two patterns of dentition are fundamentally similar, and only seem different because of variations in the relative growth-rates of the two portions of the hinge plate, which have a direct bearing on their angular relationship.

The pattern of accessory muscle scars in the two species is basically similar, but their different development in each has allowed them to be used for specific definition. An internal mould of average preservation will only show the strongest of the accessory scar impressions, and a distinctive pattern is obvious in each species. But certain well-preserved specimens of each species show numerous accessory scars in a basically similar pattern. The right valve of *Praeleda costae*, in text-fig. 9, shows the usual triangular arrangement of umbonal accessory scars. However, there is an additional scar in the middle of the base line so that this line resembles the usual pattern of umbonal scars found in *Praeleda ciae*. In text-fig. 7, a right valve of *Praeleda costae*, an additional small accessory scar is visible dorsal to the posterior adductor scar and closely adjacent to the distal posterior teeth. This appears to be the pedal scar commonly preserved in *Praeleda ciae* next to the posterior adductor scar. In text-fig. 12, a right valve of *Praeleda ciae*, a prominent umbonal accessory scar is present half-way along the umbonal cavity and adjacent to the posterior hinge plate. It is suggested that this scar is comparable to the posterior accessory scar found in *Praeleda costae* close to the posterior teeth and half-way along the series.

Discussion. Ctenodonta ciae, *C. costae*, and *C. ezquerrae* were all recorded from the Llandeilian of the Crozon Peninsula by Kerforne (1901). However, Babin (1966)



TEXT-FIG. 12. *Praeleda ciae*. Internal mould of right valve, anterior to right. The specimen is slightly crushed, but otherwise well preserved, showing numerous umbonal accessory muscle scars. The curved anterior teeth are also distinct. Specimen C.6. Llandeilo. G.R. 912441.

regarded *Ctenodonta ezquerrae* as a synonym of *Ctenodonta costae* in his sub-family Ctenodontinae. At the same time he erected a new species *Palaeoneilo ctenodontoides* in his second sub-family the Palaeoneilinae.

Babin's figures of *Ctenodonta costae* are in no way similar to photographs of the holotype from Bussaco housed in the British Museum on which the Crozon identification were based. On the contrary, his figures closely resemble photographs of the holotype of the distinctive *Ctenodonta ezquerrae*. In addition, his figures of the newly erected species *Palaeoneilo ctenodontoides* are identical to the holotype of *Ctenondonta costae*, and for these reasons it would appear that the species *Palaeoneilo ctenodontoides* Babin is invalid.

In common with the other palaeotaxodontids of the Crozon Peninsula fauna, *Ctenodonta ciae* and *Ctenodonta costae* show little similarity to the type species *Ctenodonta nasuta*, and would be best included in another genus.

The two forms show closest resemblances to *Praeleda* Pfab in general shape, dentition and accessory muscle scars. The type species *Praeleda compar* (Barrande) figured by McAlester (1968, pl. 7) appears very similar to *Ctenodonta ciae*. The dentition is in two series, and although more teeth are present to the posterior, the larger teeth are found to the anterior. A distinct pedal accessory scar is visible dorsal to the anterior adducted muscle scar, and in Paratype B (pl. 7, figs. 7 and 9) three umbonal accessory scars are also visible in a line slanting towards the anterior. The three umbonal scars are also obvious in an illustration by Pfab (1934, pl. III, fig. 2).

McAlester (1969) has listed *Praeleda* as a synonym of *Deceptrix*, but there are reasons for retaining this genus. *Praeleda compar*, *P. costae*, and *P. ciae* seem to form a group of species more closely related to each other than they are to *Deceptrix*. There is also similarity between *Praeleda* and the contemporaneous genus *Praenucula*. Whereas *Deceptrix* shows a sub-circular, equilateral form, all three species of *Praeleda*, and *Praenucula*, exhibit an anteriorly elongate shape. Although the inflation of the umbo varies within *Praeleda costae*, *P. ciae*, the anteriorly elongate shape is constant. Variation in the dentition is more common. Although the dentition of some individuals of *Praeleda* (e.g. *Praeleda costae*, text-fig. 7) is remarkably similar to *Deceptrix*, others are quite different and approach *Praenucula*. It is highly likely that these two Ordovician genera were ancestral to later Palaeozoic forms such as *Deceptrix*, and the anteriorly elongate bivalves with an internal ligament such as *Nuculanella*.

PALAEOHETERODONTIDS

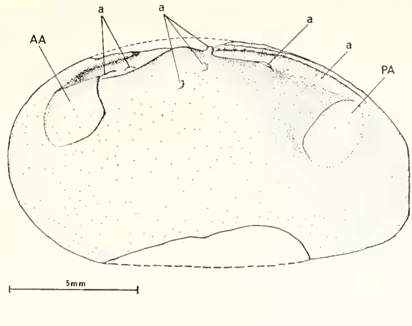
Actinodonta naranjoana (de Verneuil and Barrande) 1855

Text-figs. 13–15

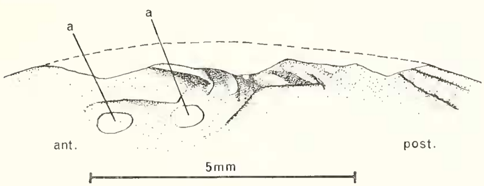
1855 *Arca naranjoana* de Verneuil and Barrande, p. 989, pl. 26, fig. 12.
1901 *Arca*? *naranjoana* Kerforne, p. 194.
1901 *Dolabra lusitanica* Kerforne, p. 194.
1923 *Arca*? *naranjoana* Kerforne, p. 180.
1966 *Actinodonta naranjoana* Babin, p. 233, text-fig. 60; pl. x, figs. 5, 7, 11.

Five to seven teeth are generally present in each valve of *Actinodonta naranjoana*. These vary in both length and orientation but give a crude impression of radiating ventrally from below the umbo, the shortest teeth being in the centre of the series (text-fig. 15). It seems unwise to use the terms 'cardinal' and 'lateral', to describe the teeth, as these have associations with the true heterodonts, and in the strictest sense imply that the lateral teeth extend posteriorly or anteriorly beyond the external ligament. This does not appear to be the case in *Actinodonta naranjoana*. Furthermore, lateral and cardinal teeth are regarded as being distinctly separate from each other, usually having different orientations. The author considers it undesirable to number these teeth in any way until the affinities of *Actinodonta* are better known.

The posterior teeth are elongate, extending from the umbo to the posterior adductor scar. They are for the most part parallel with the dorsal margin, and are crenulated



TEXT-FIG. 13. *Actinodonta naranjoana.* Internal mould of well-preserved left valve, hinge incomplete, showing general morphology and pattern of adductor and accessory muscle scars. Specimen C. 14. Llandeilo. G.R. 912441.

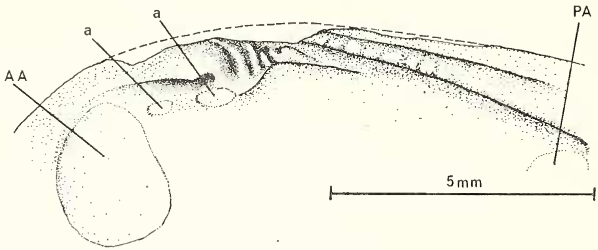


TEXT-FIG. 14. *Actinodonta naranjoana.* Internal mould of sub-umbonal and anterior hinge regions of left valve showing dentition. Part of the proximal end of the elongate socket is visible to the right. Each of the four anterior sockets (appearing as teeth) have different forms owing to varying stages in the bending of a simple ridge. Just posterior of the umbo tip are two distinct sockets that become fused in other forms. Two anterior accessory muscle scars (anterior retractor and protractor) are clearly visible anterior to the umbo. Specimen C.24. Llandeilo G.R. 912441.

along the anterior two-thirds of their length. Two such elongate teeth are present in the left valve and one in the right valve.

The most anterior tooth on the hinge is strong, and parallel with the dorsal margin. The following two or three teeth towards the umbo show a gradual change in orientation to one almost at right-angles to the dorsal margin (text-figs. 14, 15). The pattern of these teeth suggest a vague similarity to the lateral and cardinal teeth of the true heterodonts, although the analogy is incomplete. The short perpendicular teeth of *Actinodonta* are formed from the flexed tip of a longer plate that is almost parallel to the dorsal margin (see particularly text-fig. 14). There would thus appear to be 2 or 3 anterior cardinals and one anterior lateral in *Actinodonta.* However, it should be remembered that all these teeth of different orientation have in fact formed from different dental lamellae.

In the right valve of *Actinodonta*, in addition to the teeth described above, there is a short tooth below the umbo parallel to the proximal end of the long posterior tooth. This tooth provides evidence for fusion along the dental plate. In some forms two such teeth are visible below the umbo (text-fig. 14). However, in others these appear to have become reduced to a single tooth of two distinct fused components (text-fig. 15). In other forms only a single smooth-tipped tooth is visible. In a single specimen fusion has also been observed among the anterior teeth of the right valve. The ventral tips of two adjacent teeth have become fused to form a chevron-shaped tooth opening dorsally, the reverse of a similar process observed in *Cardiolaria*.



TEXT-FIG. 15. *Actinodonta naranjoana*. Internal mould of the hinge region of a left valve showing a dental plate possibly further developed than that shown in fig. 14. The anterior sockets (appearing as teeth) have become differentiated into three that are almost at right-angles to the dorsal margin, and one that is parallel to it. Between these and the long posterior socket is a single socket that clearly shows two fused sections. The anterior adductor and anterior accessory muscle scars are distinct. Specimen C.14.b. Llandeilo. G.R. 912441.

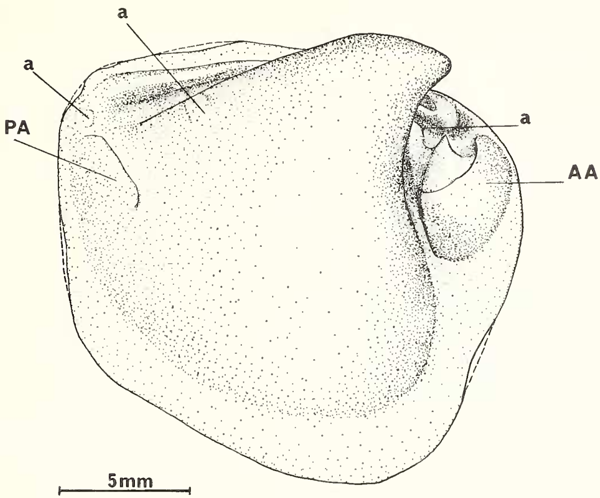
The pattern of muscle scars commonly visible in *Actinodonta naranjoana* is shown in text-fig. 13. The two closely positioned anterior accessory pedal scars visible in text-figs. 13, 14, and 15, are strongly reminiscent of the two juxtaposed anterior pedal scars present in both *Cardiolaria beirensis* and *Redonia deshayesi*. The umbonal accessory scars of *Actinodonta naranjoana* show a similarity in pattern to those observed in *Tancrediopsis ezquerrae* (text-fig. 6), and to some extent, those found in *Redonia deshayesi* (text-fig. 20).

Redonia deshayesi Rouault 1851, emend. Gouzien 1934

Text-figs. 16–21

1851 *Redonia deshayesi* Rouault, p. 364, figs. 1, 2.
1851 *Redonia duvaliana* Rouault, p. 365, fig. 1, 2.
1853 *Redonia deshayesiana* Sharpe, pl. 9, fig. 1.
1853 *Redonia duvaliana* Sharpe, pl. 9, fig. 2.
1955 *Redonia deshayesiana* de Verneuil and Barrande, pl. 16, fig. 10.
1855 *Redonia duvaliana* de Verneuil and Barrande, pl. 16, fig. 11.
1876 *Redonia deshayesiana* de Tromelin and Lebesconte, p. 641.
1876 *Redonia duvaliana* de Tromelin and Lebesconte, p. 641.

1901 *Redonia deshayesiana* Kerforne, p. 198.
1901 *Redonia duvaliana* Kerforne, p. 198.
1934 *Redonia deshayesi* Gouzien, p. 179.
1934 *Redonia duvali* Gouzien, p. 180.
1966 *Redonia deshayesi* Babin, p. 246, text-fig. 67; pl. x, figs. 13–16.



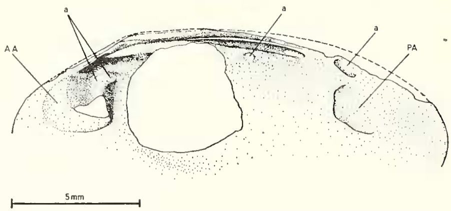
TEXT-FIG. 16. *Redonia deshayesi.* Internal mould of distorted adult right valve, showing the inequilaterally placed prosogyral umbo, and the strong anterior myophoric plate. The pallial line is simple and the anterior musculature more deeply impressed than the posterior. The mould of a chevron socket is visible anterior to the umbo, and a long socket posterior to it. Specimen A.4. Llandeilo. G.R. 831487.

The general morphology of *Redonia deshayesi* is shown in text-figs. 16–21. Previous descriptions of this genus have contained little detail on the nature and development of the dental plate.

Two teeth and two sockets are present in each valve of *Redonia deshayesi*, and all show a similar oblique orientation to the dental plate. In the left valve of an adult *Redonia deshayesi* (text-fig. 17) a strong asymmetrical chevron tooth is present below the umbo. Posterior to this and following the same oblique orientation is an elongate tooth persisting as far back as the posterior adductor muscle scar. The two limbs of the chevron tooth form an acute angle opening posteriorly, and the tooth is highest at its angulation. The dorsal limb of the chevron is extremely short, and the bulk of the tooth is formed by the longer ventral limb which lies nearly parallel to that part of the hinge immediately below the umbo.

In the right valve of an adult *Redonia deshayesi* (text-fig. 16) a strong, short, ridge-like tooth exists below the umbo posterior to a deep, chevron-shaped socket. The second tooth of this valve is situated close to the posterior adductor muscle scar, and though elongate, is shorter than the posterior tooth of the left valve. The posterior teeth of both valves terminate dorsally against what is considered to be the site of an external, opisthodetic ligament.

Whereas members of Palaeotaxodonta show an increase in the number of teeth with age, *Redonia* indicates reduction of teeth during ontogeny.



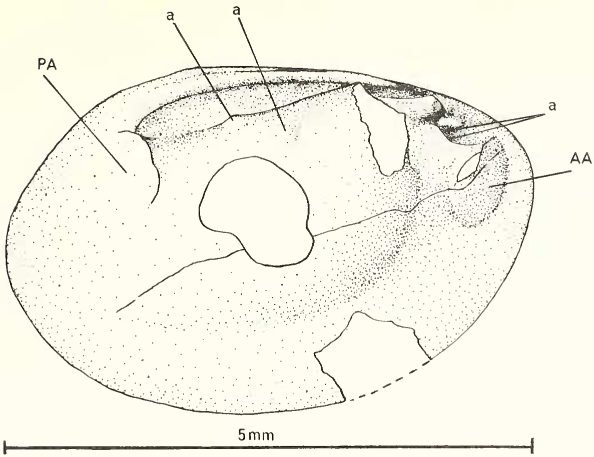
TEXT-FIG. 17. *Redonia deshayesi.* Internal mould of adult left valve showing dentition, and adductor and accessory muscle scars. Umbonal region missing. Specimen B.17. Llandeilo. G.R. 838495.

As mentioned previously, recrystallization has obliterated the detail from hinges of very young individuals. In forms approx. 5·5 mm. in length, 4 mm. in height (text-figs. 18, 19) an extra pustule-like tooth is present in each valve anterior to the teeth retained in the adult. At this size the adult teeth are already elongate, though the chevron tooth of the left valve appears only as a ridge with a very small dorsal limb curving round the anterior tip of the adjacent socket.

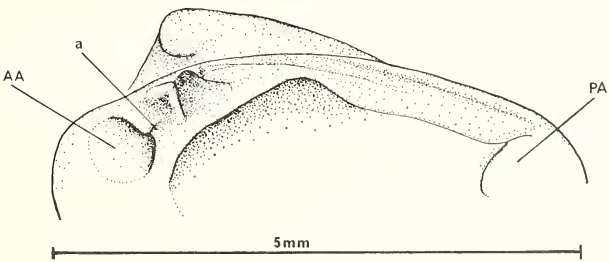
Fusion between the chevron tooth and the anterior pustule-like tooth occurs during growth of the individual. The angle of the chevron moves anteriorly as a result of this fusion and appears constricted before the process is completed (text-fig. 21). In consequence the anterior pustule-like tooth of each valve becomes obliterated, and in the adult left valve all evidence of fusion has disappeared.

Partial fusion between the posterior teeth is also obvious in *Redonia deshayesi*, similar to that already observed in *Actinodonta naranjoana*. This can be best seen by studying the internal moulds of sockets. In text-fig. 17 the moulds of two sockets (appearing as teeth) are visible, the most posterior socket mould appearing to overlap and touch that to the anterior. In text-fig. 20 the most anterior long socket mould (mould of pit-like socket also present) appears slightly bifid, and a distinct ridge extends along its dorsal flank posteriorly to merge into the second socket mould. Thus, fusion between the tips of two oblique posterior teeth appears to have taken place in the right adult valve of *Redonia* and is most obvious in younger individuals.

The musculature of *Redonia* is clearly visible in text-figs. 16–21. Two anterior pedal accessory muscle scars are visible adjacent to the adductor scar where the myophoric plate abuts the hinge plate, but these frequently have the appearance of a single narrow

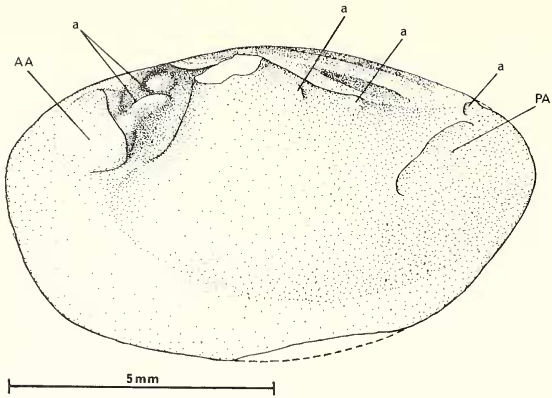


TEXT-FIG. 18. *Redonia deshayesi*. Internal mould of young right valve showing an extra socket (appearing as a tooth) to the anterior. Umbo of specimen missing. Specimen F.23.a. Llandeilo. G.R. 912441.

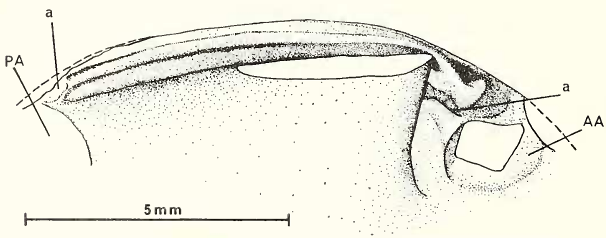


TEXT-FIG. 19. *Redonia deshayesi*. Artificial cast of specimen F.23.a shown in fig. 15. Note the strong myophoric plate and the impressed anterior adductor muscle scar with adjacent accessory scars. The distinct chevron-shaped tooth to the anterior is not present in the adult. Llandeilo. G.R. 912441.

scar with its long axis oblique to, and converging anteriorly on, the hinge plate (text-fig. 17). Well-preserved specimens of *Redonia* show these scars to be slightly oval and juxtaposed, showing a strong resemblance to those in *Cardiolaria beirensis*. A comparison with *Acila divaricata* figured by Driscoll (1964, fig. 3) would suggest that one of these scars is an anterior protractor muscle scar, and the other the anterior retractor muscle



TEXT-FIG. 20. *Redonia deshayesi.* Internal mould of young left valve showing additional socket (appearing as a pustule-like tooth) to the anterior. Adductor and accessory muscle scars are clearly visible. Specimen J.5. Llandeilo. G.R. 912441.



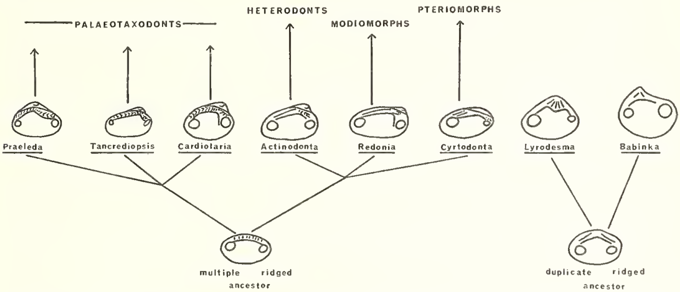
TEXT-FIG. 21. *Redonia deshayesi.* Internal mould of right valve showing form of dentition following the fusion of anterior teeth in the left valve with the mould of the chevron socket appearing constricted. Specimen F.18. Llandeilo. G.R. 912441.

scar. The smaller anterior protractor scar visible in *Cardiolaria beirensis* has not been observed in *Redonia deshayesi.* In addition, a posterior pedal accessory scar is often visible adjacent to the dorsal edge of the posterior adductor muscle scar (text-figs. 16, 17, 20). Two further accessory scars have been observed in the umbonal region (text-figs. 16, 18, 20), resembling those visible in *Actinodonta naranjoana* (text-fig. 13). It is highly likely that *Redonia* developed from a form with a dental plate similar to that of *Actinodonta.* The fusion of teeth in both forms follows a similar pattern but has been more extreme in *Redonia.*

DISCUSSION OF THE EVOLUTIONARY RELATIONSHIPS OF THE CROZON PENINSULA BIVALVE FAUNA

From the variety shown by Ordovician bivalves it seems likely that at least two, and perhaps three, ancestral stocks, with basically different dental patterns, had evolved from the early Mollusca during the Cambrian.

Following Vogel (1962) and Babin (1966) it is suggested that one ancestral stock was almost equilateral, with a dental plate bearing a simple ridge on each side of the umbo parallel to the dorsal margins. Forms such as *Lamellodonta* (Cambrian) and *Babinka* (Ordovician) probably developed from this stock. The origins of *Lyrodesma* may also lie here.



TEXT-FIG. 22. The Crozon Peninsula bivalves in a suggested Lower Palaeozoic phylogeny.

The second ancestral stock may have had a multiple-ridged dental plate, each ridge either perpendicular to the dorsal margin or slightly oblique to it (text-fig. 22). It may have shown some resemblance to juvenile forms of *Cardiolaria beirensis* (text-fig. 1).

The developing dentition of the Crozon Peninsula bivalves indicate two main lines of development from such a multiple-ridged ancestral stock (text-fig. 22). One trend is marked by a simple increment in teeth as the animal grows, the other by a tendency towards reduction in teeth by fusion and resorption. The diverse forms seen in the Ordovician fauna represent cladogenesis within these two lines. At its simplest these two lines can be viewed in terms of Douvillé's 'active' and 'burrowing' branches of bivalve evolution.

Active forms would tend to develop chevron teeth from the primitive dentition to counter the stresses produced by foraging. The most active types probably used a large foot for ploughing through sediment and labial proboscides for food collection, in a manner similar to modern *Nucula*. The primitive opisthodetic ligament and the need for a large anterior opening during retraction of the foot would encourage the development of a differentiated dental plate with larger anterior teeth as seen in *Praeleda*. The anterior part of the shell would tend to become enlarged to provide protection and accommodation. Later Palaeozoic bivalves with a reversed orientation and an internal ligament probably developed from these forms.

Another branch of this line, represented by *Cardiolaria*, may have evolved towards a secondary burrowing condition. The inherited 'active' type of dentition would become modified. With a change in the direction of growth within the valve and less frequent protrusion and retraction of the foot, there would be no tendency to increase the number of large anterior teeth. The myophoric plate and deeply impressed anterior musculature of *Cardiolaria* probably reflect its mode of life. Since the adductor muscles are used to close the shell, the anterior adductor, strengthened by the adjacent plate, suggests a more violent and sudden action by this muscle than its posterior counterpart. If *Cardiolaria* still possessed the anterior inhalent current associated with certain palaeotaxodontids, the action would produce an abrupt cleansing current out of the posterior region of the shell.

Tancrediopsis may represent a third branch, distinct from *Praeleda* and *Cardiolaria*. *Tancrediopsis* has a dentition similar to that of later siphonate nuculanids, and may have been a burrowing bivalve.

The second major line, in which tooth resorption and fusion takes place, appears to be represented by burrowing forms (text-fig. 22). The dentition of *Actinodonta* in particular suggests modification of the ancestral dental plate by elongation of its posterior components and flexing of some anterior teeth. When clear (text-figs. 14, 15), the curved anterior teeth have one long and one short limb. It is not difficult to envisage that resorption at the junction of the two limbs, to leave them isolate, would result in a dentition associated with the heterodontids.

Actinodonta and *Redonia* appear to be closely related, the latter showing a greater reduction of teeth. In addition, the general morphology of *Redonia* closely resembles that of *Cardiolaria*, particularly in the possession of a deeply impressed anterior musculature and an anterior myophoric plate. They could be regarded as homeomorphs. *Actinodonta* shows some parallels with *Tancrediopsis* in its musculature, and it is possible that both forms had posterior inhalant currents.

The cyrtodontids are generally accepted as being closely related to the later pteriomorph bivalves. From the trends reviewed in the Crozon Peninsula fauna it seems likely that they evolved during the Cambrian from the hypothetical multiple-ridged ancestor, in a slightly different direction from *Actinodonta* and *Redonia*, rather than from the duplicate ridged form.

Acknowledgements. The author gratefully acknowledges the help of the British Museum of Natural History for supplying photographs of type material. Acknowledgement is also due to Dr. R. Carter for his helpful and critical reading of the manuscript, and to Mr. D. Jones for the preparation of photographs from the original figures. The author would like to thank Professor M. Gage for the use of facilities in the Department of Geology, University of Canterbury. The author is also grateful to Dr. J. D. Bradshaw for initiating interest in the Ordovician bivalves, and for his helpful and tolerant criticism of the manuscript and many useful discussions.

REFERENCES

BABIN, C. 1966. *Mollusques Bivalves et Céphalopodes du Paléozoique Armoricain*, 472 pp. Brest.

BARROIS, C. 1886. Compte rendu de la réunion extraordinaire de la Societé dans le Finistère. *Bull. Soc. géol. Fr.* 3E, **14**, 652–78.

—— 1886. Constitution de la rade de Brest. Ibid., **14**, 678–707.

—— 1891. Mémoire sur la faune du Grès Armoricain. *Ann. Soc. géol. Nord.* **19**, 134–237.

BERNARD, F. 1896. Deuxième note sur le developpment et la morphologie de la coquille chez les lamellibranches. (Taxodontes). *Bull. Soc. géol. Fr.* 3E, **24**, 54–82.

BISHOP, A. C., BRADSHAW, J. D., RENOUF, J. T., and TAYLOR, R. T. 1969. The stratigraphy and structure of part of Western Finistère. *Q. Jl geol. Soc. Lond.* **124**, 309–48.

COX, L. R. 1960. Thoughts on the classification of the Bivalvia. *Proc. malac. Soc. London*, **34**, 60–88.

DOUVILLÉ, H. 1912. Classification des Lamellibranches. *C.R. Somm. Soc. géol. Fr.* 4E, **12**, 7.

DRISCOLL, E. G. 1964. Accessory muscle scars, an aid to protobranch orientation. *J. Paleont.* **38**, 61–6.

GOUZIEN, V. 1934. Contribution à l'étude géologique de la presqu'ile de Crozon suivant la voie ferrée de Telgruc à Camaret. *Bull. Soc. géol. Minér. Bret.* (1930), 176–91.

KERFORNE, F. 1901. *Étude de la region silurique occidentale de la Presqu'ile de Crozon.* Thèse Fac. Sci. Paris. Imp. Simon, Rennes, 234 pp.

—— 1923. Étude stratigraphique de la vallée de l'Ille entre Saint-Médard. *Bull. Soc. géol. Minér. Bret.* **41**, 78–194.

MCALESTER, A. L. 1963. Revision of the type species of the Ordovician nuculoid pelecypod genus *Tancrediopsis. Postilla*, Yale Peabody Mus. **74**, 1–19.

—— 1964. Preliminary suggestions for a classification of nuculoid bivalves. *J. Paleont.* **38**, 397–400.

—— 1968. Type species of paleozoic nuculoid bivalve genera. *Mem. geol. Soc. Amer.* **105**. 143 pp.

—— 1969. In MOORE, R. C., ed., *Treatise on invertebrate paleontology*, Part N, *Mollusca* 6, *Bivalvia*, **1** and **2** 951 pp. Geol. Soc. Am. and Univ. Kansas Press.

NEWELL, N. D. 1965. Classification of the Bivalvia. *Am. Mus. Novit.* 2206, 25 pp.

PFAB, L. 1934. Revision der Taxodonta des bohmischen silurs. *Palaeontographica*, A. **80**, 195–253.

RIBEIRO, C., SHARPE, D., and JONES, T. R. 1853. On the Carboniferous and Silurian formations in the neighbourhood of Bussaco, Portugal. *Q. Jl geol. Soc. Lond.* **9**, 135–61.

ROUAULT, M. 1850–51. Mémoires sur le terrain paléozoique des environs de Rennes. *Bull. Soc. géol. Fr.*, 2E, **8**, 358–99.

DE TROMELIN, G. and LEBESCONTE, P. 1876. Essai d'un catalogue raissoné des fossiles siluriens des departments de Maine-et-Loire, de la Loire-Inférieure et du Morbihan avec observations sur les terrains paléozoiques de l'Ouest. *Congrès. Ass. Fr. Av. Sci., Nantes* (1875), 601–61.

—— 1876. Presentation de fossiles paléozoiques du department d'Ille-et-Vilaine et note additionelle sur la faune silurienne de l'Ouest de la France. Ibid. 683–7.

DE VERNEUIL and BARRANDE C. 1855. Descriptions des fossiles trouves dans les terrains silurien et devonien d'Almaden, d'une partie de la Sierra Morena et des Montagnes de Toledo. *Bull. Soc. géol. Fr.* 2E, **12**, 182–203.

VOGEL, K. 1962. Muscheln mit Schlosszahnen aus dem spanischen Kambrium und ihre Bedeutung für die Evolution de Lamellibranchiaten. *Abhandl. Math. Nat. Kl. Acad. Wiss. und Lit. Mainz*, 192–244.

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Final typescript received 1 April 1970